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1 Running head: Metabolic rate and feed efficiency in fish

2

3 **An investigation of links between metabolic rate and feed efficiency in European sea**
4 **bass *Dicentrarchus labrax*¹**

5

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27 **ABSTRACT:** Feed efficiency (FE) is the amount of body weight gain for a given feed intake.
28 Improving FE through selective breeding is key for sustainable finfish aquaculture but its
29 evaluation at individual level is technically challenging. We therefore investigated whether
30 individual routine metabolic rate (RMR) was a predictor of individual FE in the European sea
31 bass *Dicentrarchus labrax*, a major species in European mariculture. The European sea bass
32 has three genetically distinct populations across its geographical range, namely Atlantic
33 Ocean (AT), West Mediterranean (WM) and East Mediterranean (EM). We compared FE and
34 RMR of fish from these three populations at 18°C or 24°C. We held 200 fish (62 AT, 66 WM
35 and 72 EM) in individual aquaria and fed them from *ad libitum* down to fasting. Feed
36 efficiency was assessed for an *ad libitum* feeding rate and for a fixed restricted ration (1% of
37 metabolic body weight.day⁻¹, with metabolic body weight = body weight^{0.8}). After being refed
38 12 weeks in a common tank, individual RMR was measured over 36h by intermittent flow
39 respirometry. There was a significant effect of temperature whereby fish at 18°C had greater
40 mean FE ($P < 0.05$) and lower RMR ($P < 0.001$). There was also a significant effect of
41 population, where AT fish had lower FE ($P < 0.05$) and greater RMR ($P < 0.001$) than WM
42 and EM, at both temperatures. Despite these differences in temperature and population means,
43 individual FE and RMR were not significantly correlated ($P > 0.05$). Therefore, although the

44 results provide evidence of an association between metabolic rate and FE, RMR was not a
45 predictor of individual FE, for reasons that require further investigation.

46 **Key words:** Aquaculture, genetic populations, individual rearing, oxygen consumption,
47 respirometry.

48

LIST OF ABBREVIATIONS

49 AT, Atlantic

50 BW, body weight

51 BWG, body weight gain

52 BWG_1%, body weight gain for a restricted feed intake set to 1% of metabolic body

53 weight.day⁻¹

54 dph, days post hatch

55 EM, East Mediterranean

56 FE, feed efficiency

57 FI, feed intake

58 MBW, metabolic body weight

59 MO₂, measurements of oxygen uptake

60 resBWG, residual body weight gain

61 RMR, routine metabolic rate

62 SMR, standard metabolic rate

63 WM, West Mediterranean

INTRODUCTION

64

65 Finfish aquaculture represents a promising source of sustainable animal protein for
66 growing human populations globally (Godfray et al., 2010; Froehlich et al., 2018; FAO,
67 2018). A major factor in aquaculture sustainability is, however, feeding the fishes: it is the
68 single greatest cost (Goddard, 1996) and a major determinant of environmental impact
69 (Besson et al., 2016a). Feed efficiency (FE) is the ratio between fish body weight gain (BWG)
70 and feed intake (FI); selective breeding to improve FE is a promising means to make
71 aquaculture more sustainable (Besson et al., 2014; Besson et al., 2016a). Farmed fishes are,
72 however, reared in large groups, where individual FI is technically very challenging to
73 measure (Kause et al., 2006; Grima et al., 2008). An alternative is to rear individuals singly
74 (Silverstein, 2006; Martins et al., 2011; Besson et al., 2019; Rodde et al., 2020), a technique
75 that is widely used on terrestrial livestock (Luiting and Urff, 1991; de Haer and Merks, 1992;
76 Nguyen et al., 2005; Drouilhet et al., 2016). This method has already been applied to
77 European sea bass *Dicentrarchus labrax*, a major species for finfish aquaculture in Europe
78 (Besson et al., 2019; Rodde et al., 2020). It involves holding hundreds of animals for several
79 weeks, provided with individual daily rations, with all uneaten feed carefully collected and
80 quantified each day (Besson et al., 2019; Rodde et al., 2020). In the European sea bass it
81 returned reliable estimates of individual FE, to the extent that individual FE in aquaria was
82 clearly linked to the subsequent FE of groups, groups being composed of fish graded for
83 individual FE (Besson et al., 2019). The method is, however, extremely time-consuming and
84 laborious, which impedes its application on a large scale for selective breeding programs in
85 aquaculture.

86 It is, therefore, useful to search for indirect selection criteria of individual FE, that are
87 accurate predictors and can be measured more easily and rapidly. Bioenergetics is promising
88 because it is assumed that energy intake from feed in fishes is allocated among several

89 processes, most notably maintenance metabolism, activity and growth (Warren and Davis,
90 1967; Bureau et al., 2003). It is conceivable that, for a given feed intake, the most efficient
91 individuals will be those that allocate the least energy to maintenance and activity, and the
92 most to growth. In terrestrial livestock such as cattle, sheep and poultry, there is clear
93 evidence of a negative correlation between individual metabolic rate and FE (Luiting et al.,
94 1991; Nkrumah et al., 2006; Arndt et al., 2015; Chaves et al., 2015; Paganoni et al., 2017).
95 Although there is some evidence of a link between metabolic rate and FE in groups of fishes
96 (Kingham, 1983; Zeng et al., 2017), this remains to be demonstrated at an individual level.

97 This study investigated whether individual metabolic rate, measured indirectly as rates
98 of oxygen uptake, was a predictor of individual FE in the European sea bass. In this species,
99 individual metabolic rate is negatively correlated with mass loss during fasting (Killen et al.,
100 2011; McKenzie et al., 2014), indicating a link between metabolism and non-growth energy
101 requirements, which could also relate to individual bioenergetics when feeding. Measuring
102 individual oxygen consumption by respirometry on fasted (post-prandial) fish is technically
103 quite simple and takes less than 48h per animal (McKenzie et al., 2014).

104 Three genetically distinct populations of European sea bass have been identified
105 across its natural geographical range: Atlantic (AT), West Mediterranean (WM) and East
106 Mediterranean (EM; Guinand et al., 2017). These populations started to diverge 300,000 years
107 ago (Duranton et al., 2018; Duranton et al., 2020) in environments whose temperatures
108 differed along a North-West to South-East temperature gradient (Lindgren and Håkanson,
109 2011). European sea bass farming is by coastal cage mariculture so it is valuable to
110 understand whether the populations may differ in their bioenergetics at different water
111 temperatures, with potential implications for selection programs in different areas of Europe.

112 Rodde et al. (2020) measured individual BWG and FI, over a range of feeding rates
113 from *ad libitum* down to fasting, in 200 European sea bass from AT, WM and EM

114 populations, at two temperatures, 18 and 24°C. These two temperatures are representative of
115 the coolest and warmest sites where European sea bass is reared across Europe (Vandeputte et
116 al., 2014), and correspond to the average and optimal temperatures, respectively, that
117 European sea bass undergoes when farmed in sea cages in the West Mediterranean (Person-
118 Le Ruyet et al., 2004; Besson et al., 2016b). In the present study, we evaluated the metabolic
119 rate of these individuals, by respirometry, at their acclimation temperatures. We then
120 compared this to FE, of individuals and temperature by population combinations, considering
121 when they were fed either *ad libitum* (their individual maximum energy intake) or with a
122 fixed restricted ration of 1% individual body mass per day. Fish with greater metabolic rates
123 may compensate by consuming more dietary energy than others when fed *ad libitum* but
124 would be unable to do so on a fixed ration. That is, metabolic rate might be more closely
125 related to FE when measured for a restricted ration compared to *ad libitum*. This study is, to
126 our knowledge, the first to assess whether individual metabolic rate is a predictor of
127 individual FE in farmed fish.

128 MATERIALS AND METHODS

129 *Ethical Approval*

130 Experimental procedures were approved by C2EA-36 (“Comité d'éthique en
131 expérimentation animale Languedoc-Roussillon”) under authorisations APAFiS n°
132 2018032109435819 and n° 2018100910598940.

133 *Animals*

134 Complete details of how the fish were produced, reared and evaluated for their
135 individual FE are provided in Rodde et al. (2020). Briefly, 200 European sea bass from the
136 three populations (62 AT, 66 WM and 72 EM) were produced on a single day by controlled
137 breeding at the Ifremer Experimental Aquaculture Research Station (Palavas-les-Flots,

138 France). Fish were reared at a mean (\pm SD) temperature of $16.2 \pm 0.9^\circ\text{C}$ from 0 to 97 days
139 post hatch (dph), then of $24.4 \pm 0.8^\circ\text{C}$ from 98 to 152 dph, and finally of $21.1 \pm 1.0^\circ\text{C}$ from
140 153 to 221 dph.

141 ***Measurement of Individual Bodyweight Gain and Feed Intake***

142 When fish reached 221 dph and a mean mass of $23.4 \pm 8.4\text{g}$, they were transferred to
143 an individual rearing system to estimate their individual FE. The individual rearing system
144 consisted of two independent recirculating water systems, respectively set to 18 and 24°C ,
145 each comprising 100 individual aquaria (vol. 10L), a sand filter, a biological filter and a
146 ultraviolet filter. Feed, for the whole rearing period was a commercial diet called “Neo Start
147 3” (Le Gouessant Aquaculture, Lamballe, France). This diet was comprised of 47% of crude
148 protein, 18% of crude fat, 1.5% of crude fibre, 8% of ash, 1% of phosphorus; digestible
149 energy content was 19 MJ.kg^{-1} , digestible protein/digestible energy ratio was 23 g.MJ^{-1} . Feed
150 was supplied once a day in the morning (9 a.m.) by automatic feeders set on the cover of each
151 aquarium. The 200 aquaria were arranged on racks in the same room where they were
152 shielded from visual disturbance, except once a day when uneaten feed was collected and
153 quantified for each fish. Individuals could see their conspecifics in adjacent aquaria. Each
154 aquarium received a constant supply of biofiltered aerated water at the appropriate
155 temperature: water renewal was 300% per hour and mean oxygen saturation was 114.1%
156 ($8.64 \text{ mg O}_2.\text{L}^{-1}$) and 107.1% ($7.28 \text{ mg O}_2.\text{L}^{-1}$) at 18 and 24°C , respectively. Mean water
157 salinity was 37.2‰ and 37.4‰ at 18 and 24°C , respectively, and mean water pH was 8.3 in
158 both cases. Photoperiod was artificial: 12h light/12h dark (Rodde et al., 2020).

159 To acclimate fish to individual rearing, they were first held in groups of five per
160 aquarium from 221 to 235 dph, then they were isolated and held, alone, for a further two
161 weeks of acclimation. Once so acclimated, fish were fed incremental rations until their
162 individual *ad libitum* feeding rate was identified, over three successive periods of seven days.

163 Once individual *ad libitum* feeding rate was identified, fish were exposed to six sequential
164 reductions in ration, from *ad libitum* (100%), to 80%, 60%, 40%, 20% and then 0% (fasting).
165 Fish were fed 100% *ad libitum* for 22 days, then for 10 to 11 days at the other steps; fish
166 remained in isolation for 123 days (Rodde et al., 2020). Individual BWG and FI were
167 measured at each step, to calculate fish FE *ad libitum* and at a ration of 1% individual body
168 mass per day, see below.

169 After these trials, fish were grouped into two common tanks (vol. 1000L) supplied
170 with biofiltered water at either 18°C or 24°C and fed *ad libitum* for 12 weeks. This period
171 ensured that fish were in a stable nutritional state and that physiology and behaviour were not
172 directly influenced by the feed deprivation or any stress linked to individual rearing (Dupont-
173 Prinnet et al., 2010; Rubio et al., 2010; McKenzie et al., 2014).

174 ***Metabolic Rate by Respirometry***

175 One week before respirometry, fish were distributed among three holding tanks per
176 temperature (vol. 1000L) supplied with biofiltered water. Single tanks were fasted for 24h
177 sequentially, and then, in the afternoon, up to 32 fish were netted, identified by a passive
178 integrated transponder tag and weighed. The three tanks meant that fish were not disturbed by
179 netting more than once every 72h. They were then placed into individual semi-transparent
180 respirometry chambers (volume either 1.8 or 3.0L) according to their size, such that they were
181 free to move easily, and left for 12h (overnight) to recover from handling. There were 32
182 respirometry chambers, placed submerged on two polyvinyl chloride trays (100 x 200 x 28
183 cm) supplied with aerated biofiltered seawater at either 18°C or 24°C. The trays were shielded
184 behind opaque black plastic to avoid visual disturbance, with the fish in dim light at an
185 artificial photoperiod of 12h light/12h dark. In that system, individuals will have been aware
186 of their conspecifics in adjacent chambers.

187 Measurements of oxygen uptake (MO_2) were made by intermittent stopped-flow
188 respirometry (Steffensen, 1989) as described in McKenzie et al. (2014), but with a 15 minute
189 cycle comprising eight minutes stopped flow and seven minutes flushing with aerated water.
190 Water oxygen levels in the chambers were measured and recorded every ten seconds by
191 optodes (Firesting OXROB10 oxygen sensors, www.pyroscience.com) and associated oxygen
192 meter (Firesting FSO2-O4) and software (Pyro Oxygen Logger). During stopped flow,
193 oxygen saturation in the chambers declined due to consumption by the fish, MO_2 was
194 calculated as $mg\ O_2.kg^{-1}.h^{-1}$ considering the volume of the chamber and the solubility of
195 oxygen in seawater at 18 or 24°C and a salinity of 37‰ (Steffensen, 1989; Dupont-Prinet et
196 al., 2010). After the 12h recovery from handling, measurements were collected for 24h on
197 undisturbed fish. Upon removal of a batch from their chambers, background oxygen
198 consumption due to bacterial respiration was measured over 20 min in the sealed chambers
199 (Svendsen et al., 2016), this represented about 2% of the total oxygen consumption by the
200 fish, so no correction was applied.

201 *Data Analysis and Statistics*

202 All statistical analyses were performed with R software (R Core Team, 2018). The
203 normality of residuals was checked using the quantile-quantile method (comparing residuals
204 quantiles with theoretical normal quantiles). The homoscedasticity and independence of the
205 residuals were checked by comparing the residuals with the fitted values from the models.
206 Linear mixed models and tests associated to these models were performed using R packages
207 “lme4” (Bates et al., 2015) and “lmerTest” (Kuznetsova et al., 2017).

208 ***Feed efficiency: Relationship between BWG and FI.*** The measures of BWG and FI
209 were standardized to (divided by) metabolic body weight (MBW) instead of body weight
210 (BW), based upon a mass exponent for metabolic rate of 0.8 in European sea bass (MBW =
211 $BW^{0.8}$; Lemarié et al., 1992; Lupatsch et al., 2003; Rodde et al., 2020). Both BWG and FI

212 were then expressed as a percentage of MBW. The following repeated measures linear mixed
213 model was used to estimate individual FE as residual BWG (resBWG) when fish were fed *ad*
214 *libitum*:

$$215 \text{ BWG}_{ij} = \text{intercept} + \text{slope} * \text{FI}_{ij} + A_j + B_j * \text{FI}_{ij} + \text{resBWG}_{ij}$$

216 where BWG_{ij} and FI_{ij} are, respectively, the BWG and FI at step i (i between 1 for *ad libitum*
217 and 6 for fasting) for animal j , A_j and B_j are the random effects of the animal j , respectively,
218 associated with intercept and slope, with $A_j \sim N(0; \sigma_a^2)$, with $B_j \sim N(0; \sigma_b^2)$ and resBWG_{ij} the
219 residual of the model ($\text{resBWG}_{ij} \sim N(0; \sigma_e^2)$). From a biological point of view, the greater the
220 resBWG, then the more efficient the individual. The model was calibrated on all the data from
221 the six different feeding rates to increase its robustness, although only resBWG_{ij} (resBWG *ad*
222 *libitum*) were to be extracted from the model for further analyses.

223 Then, the following linear model was used for each fish to estimate the intercept and
224 slope of the linear relationship between its BWG and FI:

$$225 \text{ BWG}_i = \text{intercept} + \text{slope} * \text{FI}_i + \varepsilon_i$$

226 where BWG_i and FI_i are respectively the BWG and FI at step i (i between 1 for *ad libitum* and
227 6 for fasting) for each fish, and ε_i the residual ($\varepsilon_{ij} \sim N(0; \sigma_e^2)$). The intercept and slope of this
228 relationship permitted to predict for each fish its BWG (in % of MBW) for a restricted FI set
229 to 1% of MBW.day⁻¹, abbreviated as BWG_1%, with $\text{BWG}_1\% = \text{intercept} + \text{slope} * 1$.

230 **Calculation of Metabolic Rates.** Rates of oxygen uptake were corrected to (divided
231 by) MBW, as per the measures of BWG and FI. Routine metabolic rate (RMR), defined as the
232 metabolic rate of post-absorptive, undisturbed, resting animals at their acclimation
233 temperature, which also includes the costs of random activity and the maintenance of posture
234 and equilibrium (Killen et al., 2011), was taken as the mean rate of MO₂ over 24h. Standard
235 metabolic rate (SMR), defined as the minimal energetic cost of living for an ectotherm at their

236 acclimation temperature, was estimated as the 0.25 quantile of MO₂ values over the 24h
237 period (Chabot et al., 2016).

238 ***Variation in Phenotypic Traits between Temperatures and among Populations.*** The
239 following linear model was used to determine the variation of each trait at temperature and
240 population levels:

$$241 Y_{ijk} = \mu + T_i + P_j + TP_{ij} + \varepsilon_{ijk}$$

242 where Y_{ijk} is the phenotypic trait considered at temperature i (18°C or 24°C), for genetic
243 population j (AT, WM or EM) and animal k; μ is the general mean, T is the fixed effect of
244 temperature, P is the fixed effect of population, TP the interaction of these two effects, and ε_{ijk}
245 the residuals ($\varepsilon_{ijk} \sim N(0; \sigma_e^2)$). Regarding the three populations, their pairwise differences were
246 further explored using Tukey post-hoc test.

247 ***Link between Feed Efficiency and Metabolic Rate among Individuals.*** Pearson's
248 correlation coefficient was estimated between traits of FE and metabolic rate, for each single
249 temperature by population combination.

250 RESULTS

251 Among the 200 fish held, six died before the phenotyping period because they jumped
252 out of their aquarium (five AT at 18°C and one AT at 24°C). Of the 194 fish that were
253 phenotyped in the aquaria, 46 failed to have a positive growth rate when fed *ad libitum*: seven
254 AT out of 28, five WM out of 34 and six EM out of 37 at 18°C; 11 AT out of 28, 13 WM out
255 of 32 and four EM out of 35 at 24°C. The resBWG and metabolic rate were not estimated for
256 fish that lost weight *ad libitum*. For ethical reasons, if a fish had lost weight when fed *ad*
257 *libitum*, or to 80%, 60% or 40% of *ad libitum*, the next step was fasting, with the fish then
258 removed from the experiment. Moreover, five fish (two AT at 18°C, two AT at 24°C and one
259 WM at 24°C) did not eat at all when fed *ad libitum* (< 1% of their BW over the 22 days) and
260 were therefore removed from the experiment, without any fasting step. The individual linear

261 model to calculate BWG_1% was only applied to the 107 fish that were successively
262 phenotyped for at least 100%, 80%, 60% and 0% of *ad libitum* feeding rate, to have at least
263 four data to calibrate the individual linear model (Rodde et al., 2020).

264 Mean mass at the end of the individual rearing period was $31.3 \pm 12.0\text{g}$ at 18°C and
265 $35.4 \pm 11.4\text{g}$ at 24°C . After 12 weeks of *ad libitum* refeeding into common tanks, a threefold
266 and fourfold increase in body mass was observed at 18°C and 24°C , respectively: when
267 respirometry was performed, the mean mass was $99.0 \pm 29.7\text{g}$ at 18°C and $146.2 \pm 40.4\text{g}$ at
268 24°C . Among the 148 fish that were successfully phenotyped *ad libitum*, 120 fish (18 AT, 19
269 WM and 25 EM at 18°C and 14 AT, 17 WM and 27 EM at 24°C) had their metabolic rate
270 successfully estimated. Moreover, among the 107 fish that had their BWG_1% estimated, 92
271 fish (14 AT, 13 WM and 22 EM at 18°C and 7 AT, 12 WM and 24 EM at 24°C) had their
272 metabolic rate successfully estimated.

273 ***Variation in Phenotypic Traits between Temperatures and among Populations***

274 Firstly, resBWG (*ad libitum* feeding rate) as well as BWG_1% were significantly
275 different between temperatures ($F_{1,126} = 4.75$, $P = 3.11 \times 10^{-2}$ and $F_{1,103} = 8.88$, $P = 3.59 \times 10^{-3}$,
276 respectively) and among populations ($F_{2,126} = 7.25$, $P = 1.05 \times 10^{-3}$ and $F_{2,103} = 12.32$, $P =$
277 1.59×10^{-5} , respectively). Both resBWG and BWG_1% were greater at 18°C than at 24°C ,
278 while the AT fish had significantly lower resBWG and BWG_1% than WM fish ($P =$
279 2.30×10^{-2} and 6.73×10^{-3} with Tukey post-hoc test, respectively) and EM fish ($P = 1.02 \times 10^{-3}$
280 and $P = 2.79 \times 10^{-5}$ with Tukey post-hoc test, respectively). These traits were not significantly
281 different between WM and EM fish ($P = 0.70$ and $P = 0.31$, respectively). There was no
282 temperature by population interaction ($F_{2,124} = 0.58$, $P = 0.56$ and $F_{2,101} = 0.21$, $P = 0.81$, for
283 resBWG and BWG_1%, respectively).

284 Regarding RMR and SMR, means for temperatures and populations are presented in
285 Table 1, with RMR values in Fig. 1. Firstly, RMR was positively and strongly correlated with

286 SMR, whatever the temperature by population combination ($r = 0.60-0.97$). Thus, we chose to
287 focus only on RMR results because SMR has very similar variations. Within each temperature
288 by population combination, individual RMR was moderately variable with a CV
289 ($100 \times \text{standard deviation} / \text{mean}$) between 9.8 and 14.8%. Moreover, RMR differed
290 significantly by temperature, with fish reared at 18°C having lower RMR ($F_{1,116} = 130.89$, $P <$
291 2.2×10^{-16}), but also by population ($F_{2,116} = 14.02$, $P = 3.52 \times 10^{-6}$), whereby AT fish had a
292 significantly greater RMR than WM and EM fish ($P = 1.95 \times 10^{-4}$ and $P = 1.81 \times 10^{-4}$
293 respectively using Tukey post-hoc test). In contrast, the RMR of WM and EM fish was not
294 significantly different ($P = 0.94$). Moreover, there was no interaction effect between
295 temperature and population on RMR ($F_{2,114} = 1.67$, $P = 0.19$).

296 *Correlation between Performance and RMR*

297 As illustrated in Fig. 2, a link between RMR and resBWG as well as BWG_1%
298 appears at temperature and populations levels. Indeed, fish at 18°C have a lower RMR and
299 greater resBWG and BWG_1% than 24°C. Similarly, AT fish have a greater RMR and lower
300 resBWG and BWG_1% than WM and EM fish.

301 At the individual level, the correlations between RMR and resBWG ranged from -0.33
302 to 0.39 among the various temperature by population combinations (Fig. 3), but none of them
303 was significant ($P > 0.05$ in all cases). Similarly, the correlations between RMR and
304 BWG_1% ranged from -0.43 to 0.15 among the various combinations (Fig. 4) and none of
305 them was significant ($P > 0.05$ in all cases).

306 **DISCUSSION**

307 This study is the first to attempt to relate individual variation in FE to metabolic rate in
308 a farmed fish, the European sea bass. The results revealed effects of temperature and
309 population on FE that could be linked to differences in RMR. No such relationships were
310 observed at an individual level.

311 ***Link between Feed Efficiency and RMR between Temperatures and among Populations***

312 The initial hypothesis made was that the most efficient fish, for a given feeding rate
313 (1% of MBW.day⁻¹ in the present study), were those allocating the least energy to
314 maintenance and activity, resulting in more available energy for growth. Present RMR results
315 tend to valid this hypothesis between temperatures and among populations. Indeed, RMR
316 differed in a consistent way with BWG_1%: fish at 18°C were more efficient for 1% of
317 MBW.day⁻¹ and had a lower RMR than at 24°C, AT fish were less efficient for 1% of
318 MBW.day⁻¹ and had a greater RMR than WM and EM fish.

319 Given that we estimated resBWG for fish fed *ad libitum*, it is perhaps surprising that it
320 was also linked to RMR. It might have been suggested that fish with greater metabolic costs
321 (i.e. RMR) would have compensated by increasing their *ad libitum* energy intake. However,
322 our resBWG data suggest metabolic costs outweighed any potential compensation through an
323 increased energy intake. This contrasts with Chinese crucian carp (*Carassius auratus*) where
324 fish with greater RMR were less efficient under a restricted feeding rate but more efficient
325 when fed at *ad libitum* (Zeng et al., 2017). This difference in results may be explained by the
326 fact that fish were reared as a group by Zeng et al. (2017) but individually in the present
327 study. Indeed, in the present study, *ad libitum* FI ranged from 0.53 to 0.73% and from 0.85 to
328 1.12% of BW.day⁻¹ at 18°C and 24°C, respectively (Rodde et al., 2020). This is low compared
329 to what could be expected in group rearing: around 1.1% and 1.7% of BW.day⁻¹ at 18°C and
330 24°C, respectively, according to the model developed by Lanari et al. (2002) for European sea
331 bass. It suggests that European sea bass do not achieve their full feed consumption potential
332 during individual rearing.

333 The fact that RMR was greater in fish reared at 24°C than in those reared at 18°C is
334 not surprising: oxygen consumption is known to increase with temperature in every fish
335 species (meta-analysis by Clarke and Johnston, 1999), including European sea bass

336 (Claireaux and Lagardère, 1999). In contrast, it is very interesting that AT fish had a greater
337 RMR than the two Mediterranean populations. This has, to our knowledge, never been
338 reported before, although they are known to be genetically distinct (Duranton et al., 2018) and
339 differ in other phenotypic traits such as growth, sex ratio, muscle fat or resistance to viral
340 nervous necrosis (Guinand et al., 2017; Doan et al., 2017; Vandeputte et al., 2019). One event
341 that may have provided a genetic basis for differences in metabolic rate among the
342 populations is an ancient admixture between the Atlantic European sea bass and the closely
343 related *Dicentrarchus punctatus* (Duranton et al., 2020). This led to the subsequent rapid
344 fixation of some *D. punctatus* alleles in the Atlantic *D. labrax* and to the establishment of
345 reproductive isolation barriers between Atlantic and Mediterranean populations (Duranton et
346 al., 2020).

347 The phenotypic traits underlying such differences among populations in metabolic rate
348 still need to be determined. It seems unlikely that variation is due to behavioural differences,
349 because RMR was so strongly correlated with SMR, which indicates that animals were
350 routinely very close to their basal metabolism. This can be explained by the fact that fish
351 exhibited little swimming activity while in the individual respirometry chamber. Even if the
352 experimental set-up avoided any disturbance from the outside, such little activity appears
353 surprising. This may be due to the fact these fish had already experienced 123 days in isolated
354 aquaria before being evaluated for RMR. Thus, the fish used here were probably more
355 acclimated to isolation than usual, resulting in a low swimming activity. Other factors may be
356 account for the RMR differences among populations. For instance, greater RMR might be
357 associated to bigger sizes of metabolically expensive organs such as heart, liver or brain
358 (Konarzewski and Książek, 2013), greater mitochondrial density (i.e. energy consumption per
359 unit mass of tissue), greater activity of mitochondrial enzymes or lower ATP production
360 efficiency (i.e. ATP produced per unit consumption of oxygen; Norin and Metcalfe, 2019).

361 Investigating these various hypotheses could provide a better understanding of the factors
362 underlying RMR variation among populations.

363 ***Link between Feed Efficiency and RMR at Individual Level***

364 Differences observed between temperatures and among populations revealed a
365 consistent link between high FE performance and low RMR, whatever the feeding rate. In
366 contrast, no correlation appeared at the individual level, no matter if the feeding rate was
367 restricted (1% of $MWB \cdot day^{-1}$) or not (*ad libitum*). Nevertheless, there is a need for further
368 investigation before concluding that RMR is of no use to improve FE in a selective breeding
369 program.

370 Firstly, only genetic correlations permit the conclusion whether a trait can be selected
371 indirectly using another trait. At the individual level, a CV of 9.8 to 14.8% was found for
372 RMR. Similarly, Killen et al. (2011) found a CV of 13% for European sea bass RMR,
373 measured by the same respirometry method and then corrected for metabolic body weight.
374 There is a need to determine whether this phenotypic variation in RMR has any heritable
375 genetic component. However, setting up an experimental design to estimate genetic
376 correlations is technically challenging. The number of fish phenotyped for both FE and RMR
377 would need to be multiplied by at least four or five in comparison with the present study.

378 Moreover, fish BWG and FI performance were measured before RMR, and not
379 simultaneously. The time lapse between these measurements was 12 weeks and fish had their
380 weight multiplied by four, so their development stage was not similar, and this may explain
381 why a correlation was not found. Metabolic rate estimation is known to have a moderate short
382 term-repeatability in European sea bass ($r = 0.48$ for measurements separated by 20 minutes;
383 Marras et al., 2010), but its longer term repeatability is, to our knowledge, unknown in this
384 species. This is problematic because long-term repeatability of metabolic rate may be species-
385 specific. For instance, it was reported as high ($r = 0.68$ for measurements separated by 17

386 weeks) in Atlantic salmon *Salmo salar* (McCarthy, 2000) but as very low ($r = 0.093$ for
387 measurements separated by 15 weeks) in brown trout *Salmo trutta* (Norin and Malte, 2011).
388 Similarly, the long-term repeatability of individual FE is completely unknown in the
389 European sea bass. Since it is not technically feasible to estimate individual FE and RMR
390 simultaneously, further investigation of both traits' long-term repeatability is needed.

391 It is also unknown whether the type of reserves, i.e. proteins or lipids, on which each
392 fish relies the most to produce its energy. Indeed, lipids provide twice as much energy as
393 proteins do for an equal weight. Thus, to ensure equal maintenance costs, fish degrading
394 lipids will consume a lower mass of reserves than fish degrading proteins. For instance,
395 McKenzie et al. (2014) reported that European sea bass relying on proteins rather than on
396 lipids to produce energy while fasting were losing more weight. Consequently, a link between
397 the main type of reserves used and individual FE may exist. In particular, AT fish muscle fat
398 content is greater than in the Mediterranean populations (Vandeputte et al., 2014; F. Allal,
399 personal communication, 2020). Thus, AT fish might use their lipid reserves less than
400 Mediterranean populations (and so they tend to accumulate them), degrading their protein
401 reserves instead. This could explain why AT fish are ultimately less efficient. This hypothesis
402 is supported by results reported in several species such as pig or rainbow trout showing the
403 most efficient animals had the lowest muscle fat content (Kamalam et al., 2012; Kause et al.,
404 2016; Knap and Kause, 2018).

405 Our results demonstrated variation among European sea bass populations regarding
406 oxygen consumption, in addition to the well-known effect of temperature on this trait.
407 Between temperatures and among populations, fish with a lower oxygen consumption were
408 more efficient. However, at the individual level, no significant correlation was found. Further
409 investigation is still required to fully understand the link between individual FE and oxygen
410 consumption in fish.

411

DISCLOSURES

412 The authors declare that they have no conflict of interest.

413

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556 **Tables and Figures**

557 **Table 1.** Mean \pm standard deviation (100*standard deviation/mean) of routine metabolic rate
558 (RMR), standard metabolic rate (SMR) and weight at respirometry. Results are presented for
559 Atlantic (AT), West Mediterranean (WM) and East Mediterranean (EM) populations reared at
560 18°C or 24°C. Within each combination of temperature by population, the correlation
561 between RMR and SMR is given with P-value, as well as the number of fish

562 **Fig. 1.** Routine metabolic rate (RMR) values observed for each combination of temperature
563 by population. Results are presented for Atlantic (AT), West Mediterranean (WM) and East
564 Mediterranean (EM) populations reared at 18°C or 24°C. In the box and whisker plots
565 presented, the box lower and upper limits are respectively the 0.25 and 0.75 quantiles of the
566 RMR data and the box is divided by the median of the values. The whiskers lower and upper
567 ends are respectively the lowest and greatest RMR values. Dots represent each fish RMR

568 **Fig. 2.** A) Residual body weight gain at *ad libitum* feeding rate as a function of routine
569 metabolic rate (RMR) among temperature by population combinations. B) Predicted body
570 weight gain as a function of RMR among temperature by population combinations. Predicted
571 body weight gain is expressed in % of metabolic body weight (MBW) and is corresponding a
572 level of feed intake set to 1% of MBW.day⁻¹. Results are presented for Atlantic (AT), West
573 Mediterranean (WM) and East Mediterranean (EM) populations reared at 18°C or 24°C.
574 Horizontal and vertical bars associated to each point are corresponding to standard errors

575 **Fig. 3.** Individual residual body weight gain at *ad libitum* feeding rate as a function of
576 individual routine metabolic rate (RMR). Results are presented for Atlantic (AT), West
577 Mediterranean (WM) and East Mediterranean (EM) populations reared at 18°C or 24°C. The
578 straight lines represent the linear regressions of individual residual body weight gain as a
579 function of individual RMR in each case

580 **Fig. 4.** Individual predicted body weight gain as a function of individual routine metabolic
581 rate (RMR). Predicted body weight gain is expressed in % of metabolic body weight (MBW)
582 and is corresponding a level of feed intake set to 1% of MBW.day⁻¹. Results are presented for
583 Atlantic (AT), West Mediterranean (WM) and East Mediterranean (EM) populations reared at
584 18°C or 24°C. The straight lines represent the linear regressions of individual predicted
585 weight gain as a function of individual RMR in each case

586

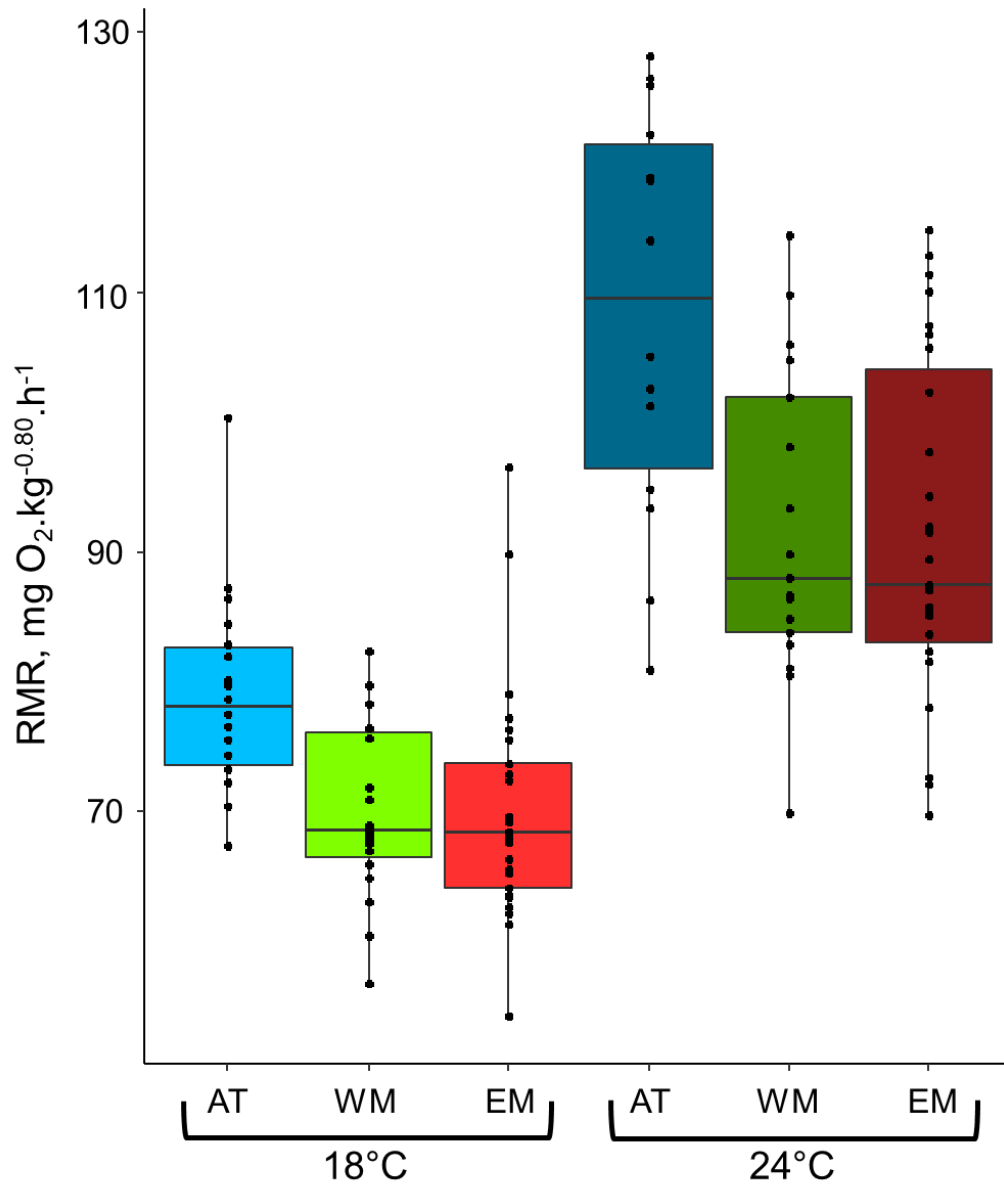
587 **Table 1**

588 Mean \pm standard deviation (100*standard deviation/mean) of routine metabolic rate (RMR),
 589 standard metabolic rate (SMR) and weight at respirometry. Results are presented for Atlantic
 590 (AT), West Mediterranean (WM) and East Mediterranean (EM) populations reared at 18°C or
 591 24°C. Within each combination of temperature by population, the correlation between RMR
 592 and SMR is given with P-value, as well as the number of fish

	RMR, mg O₂.kg^{-0.8}.h⁻¹	SMR, mg O₂.kg^{-0.8}.h⁻¹	Weight at respirometry, g	Correlation between RMR and SMR (P-value)	Number of fish
<i>Combinations</i>					
AT x 18°C	78.7 \pm 8.0 (10.2)	67.8 \pm 4.7 (7.0)	107.6 \pm 34.9 (32.5)	0.60 (P < 0.01)	18
WM x 18°C	70.1 \pm 6.9 (9.8)	63.8 \pm 5.8 (9.1)	80.0 \pm 20.8 (25.9)	0.88 (P < 0.001)	19
EM x 18°C	70.3 \pm 9.0 (12.9)	65.4 \pm 7.2 (11.0)	107.2 \pm 25.5 (23.8)	0.92 (P < 0.001)	25
AT x 24°C	108.5 \pm 15.7 (14.5)	86.8 \pm 13.9 (16.0)	142.2 \pm 39.8 (28.0)	0.83 (P < 0.001)	14
WM x 24°C	91.9 \pm 12.1 (13.2)	80.7 \pm 10.4 (12.8)	125.5 \pm 26.9 (21.4)	0.91 (P < 0.001)	17
EM x 24°C	91.3 \pm 13.6 (14.8)	80.8 \pm 13.1 (16.2)	161.3 \pm 42.7 (26.5)	0.97 (P < 0.001)	27

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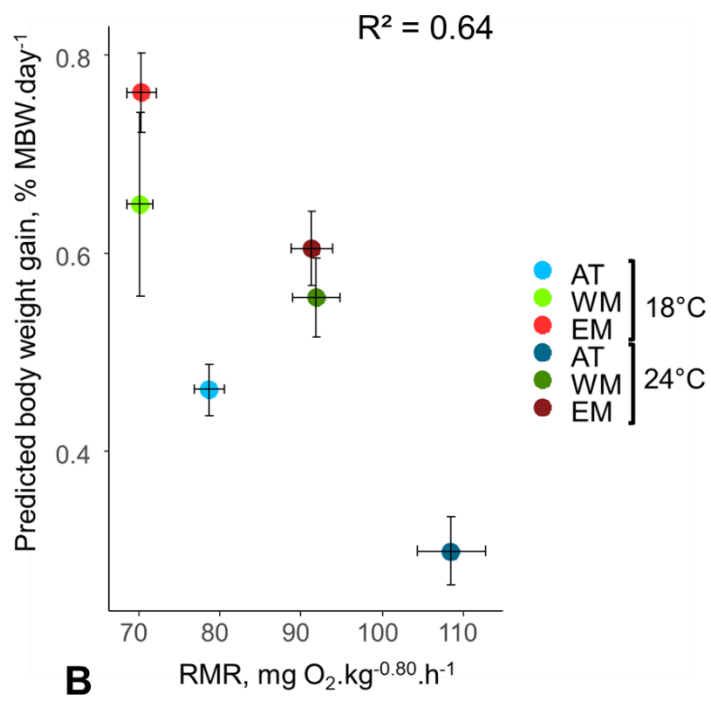
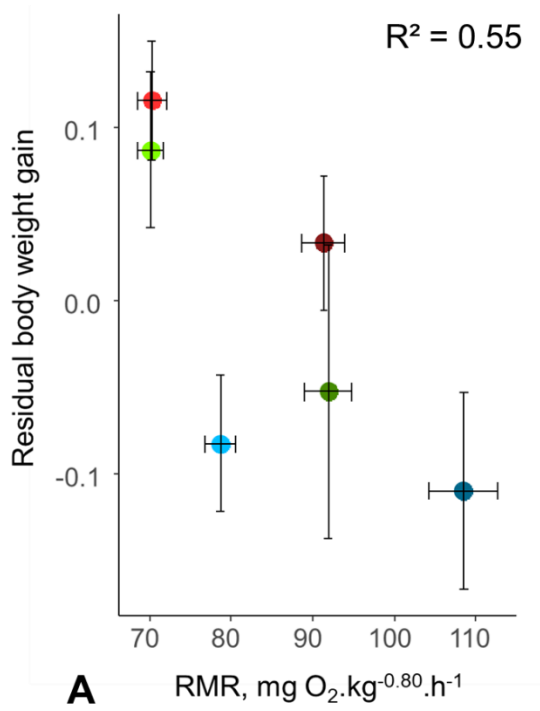
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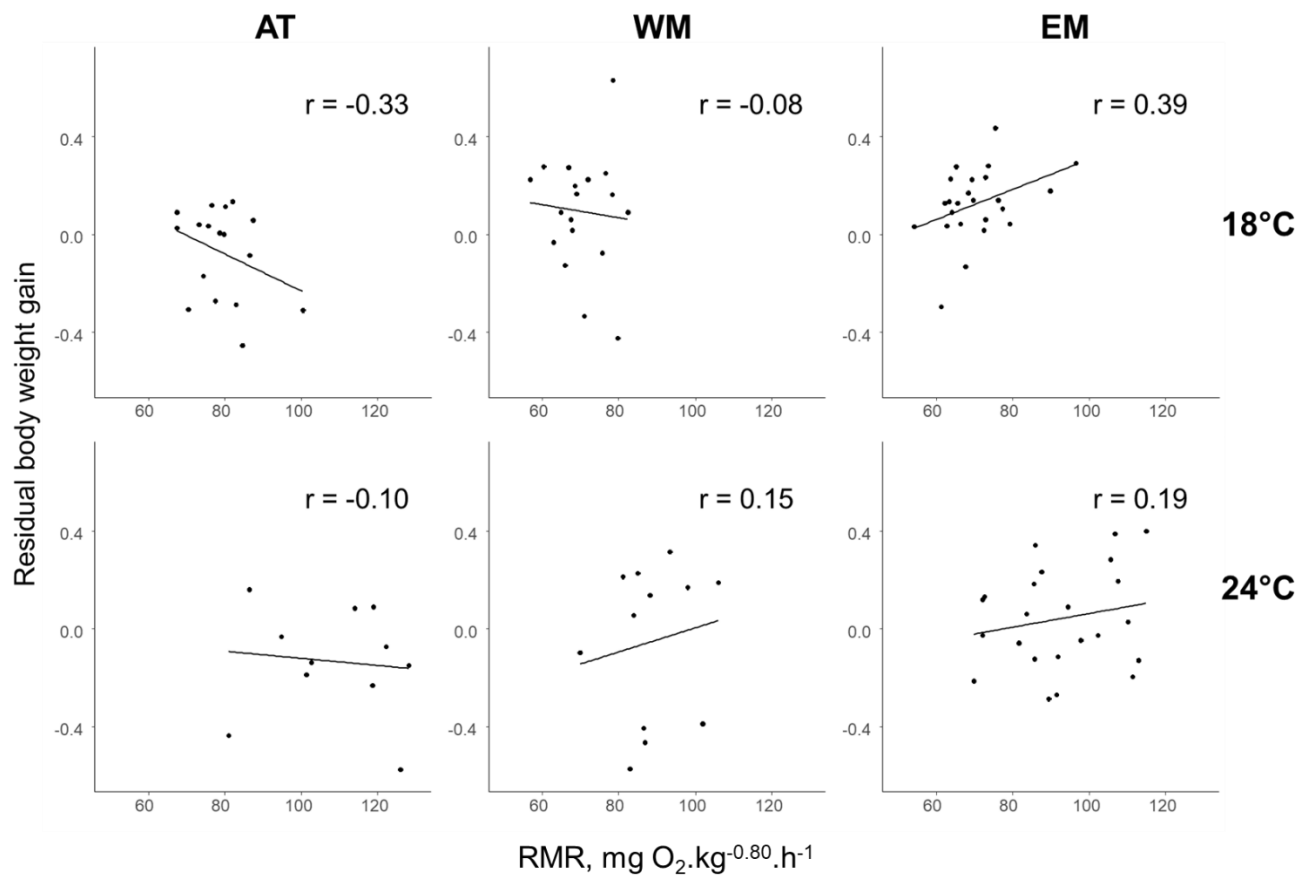
Fig. 1.



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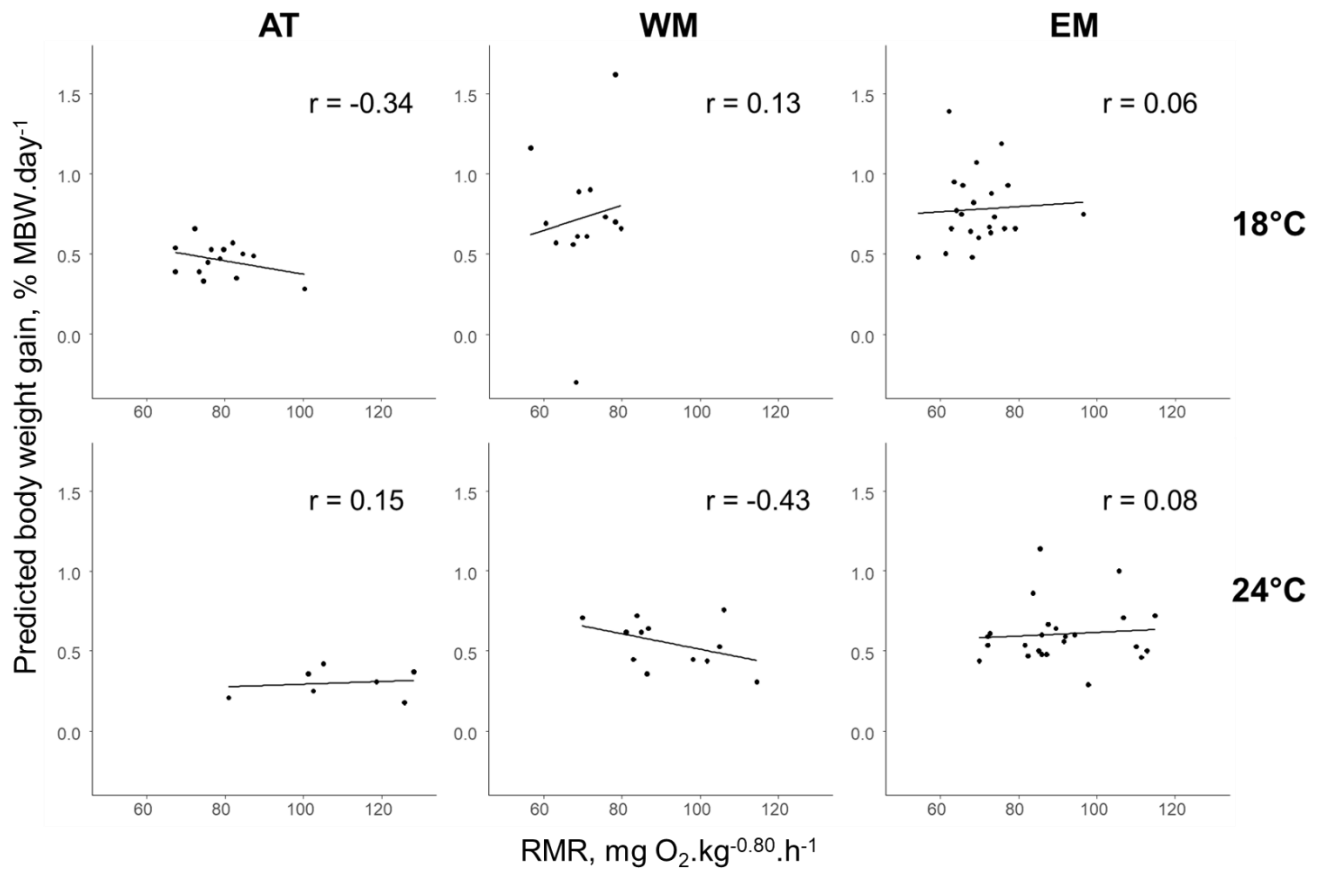
Fig. 2.



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Fig. 3.



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Fig. 4.